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The Anatomy and Development of the Eyes and Sub-Neural Gland of Salpidae, with certain considerations as to the homology of the nervous system in the different groups of Tunicata.

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The Anatomy and Development of the Eyes and Sub-Neural Gland of Salpidae, with certain considerations as to the Homology of the Nervous System in the different groups of Tunicata.

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The extensive collections of Salpa made by the United States Fish Commission, which were placed at the disposal of Professor Brooks and upon which the investigations here reported were made, include the following species:—

Cyclosalpa pinnata, Forsk., solitary and chain form.

Cyclosalpa Chamissonis Brooks, chain form

Salpa cylindrica Cuv., solitary and chain

forms.

Salpa runcinata-fusiformis, Cham., solitary and chain forms.

Salpa Africana-maxima, Forsk., solitary and chain forms.

Salpa costata-Tilesii, Quoy and Gaim., solitary and chain forms.

Salpa hexagona, Quoy and Gaimard, solitary and chain forms.

Salpa democratica-mucronata, Forsk., solitary and chain forms.

Salpa cordiformis-zonaria, Quoy and Gaim., solitary and chain forms.

Salpa scutigera-confoederata, Cuv., solitary and chain forms.

Salpa bicaudata (?), Quoy and Gaim., chain form, (probably the bicaudata is a distinct *variety* of Salpa scutigera-confoederata.)

Up to the present time no comparative study of the eyes of the different species of Salpa has been made. Perhaps this is not strange, for the group Salpidae is so highly specialized that a knowledge of the eye of this group is not likely to throw much light upon the relations between the visual organs of the Chordata in general. A very casual glance at the structure of the eye in the different species of Salpa is enough, however, to show that such a comparative study is likely to prove of considerable value within the group.

So far as I can learn, the ciliated funnel is the only structure as yet described in Salpa, that has been regarded as homologous with any part of the sub-neural gland of Ascidians. In the course of the present paper I shall describe certain other structures that seem

it has the closest relation to the Ascidian gland itself and to the lateral ducts from the gland of Phallusia mammillata to the peribranchial chamber. I shall try to show also that a certain part of the ganglion of Salpa is homologous with the sub-neural gland of Ascidians rather than with any part of the Ascidian ganglion.

Section I The Eye

Special Part

The most noticeable feature of the anatomy of the eye of Salpa and Cyclosalpa is its great uniformity of shape throughout the solitary forms of the different species and the strongly contrasted diversity of form that is shown in the chain individuals of these same species. These diverse forms are constant and characteristic for each species. In no case does the shape of the eye in the chain form agree with

the shape in the solitary form of the same, or even the species. The variations in histological structure must be described in detail. The eye of the chain individual is closely related to that of the solitary salpa, for it passes through an ontogenetic stage corresponding in shape to the adult condition of the latter. The eye of the solitary Salpa must then be regarded as the type from which the eye of the chain Salpa has diverged to a greater or less extent in the different species. The eye of the chain salpa is not however, in all cases a simple structure with a single origin, as is the case in the solitary form, but, in several species distinct eyes are developed, or new portions of distinct origin are added to that part of the eye which is homologous with the eye of the solitary form.

The Anatomy of the Eye of Cyclosalpa pinnata, solitary form.

On the dorsal surface of the ganglion of the solitary form of Cyclosalpa pinnata there is a ridge shaped like a horse-shoe, with the open end of the horse-shoe anterior. This ridge like the ganglion is composed of a cellular, peripheral portion and a non-cellular core; the cellular portion of the one being continuous with that of the other, while the core of the ridge is continuous with the central non-cellular portion of the ganglion. The height of the ridge above the ganglion is a little less than its width. On the anterior face of the posterior part of the ridge and on the inner faces of its two anterior limbs the cells are modified to form the retina of the eye. The eye thus in every part faces toward the mid-dorsal point of the brain. The retina

is formed from the more dorsal cells of the inner half of the optic ridge. The cells of the outer layer of the ridge and of the ventral part of the inner half resemble the cells of the ganglion.

The ectoderm lies on the outer and dorsal surface of the optic ridge, but does not descend to the ganglion between the anterior limbs of the ridge. Between the dorsal surface of the ganglion, the optic ridge and the ectoderm there is a space which is a blood lacuna. This space, the optic chamber, is nearly shut off from the space in which the ganglion lies by a membrane which extends from the ganglion at the base of the optic ridge, not on all [illegible] the [illegible]. The delicate membrane that clothes the ganglion is continued over the optic ridge. The membrane that closes off the optic chamber from the space in which

the brain lies is continuous, on the one hand with the membrane that covers the ganglion and eye and, on the other hand, with the basement membrane upon which the ectoderm cells abutt. That portion of the ectoderm which covers the eye and bounds the optic chamber on its inner wall I call the sheath.

The histological structure of the retina is the same in all regions. The retina consists of three kinds of cells: (1) rod cells; (2) intermediate cells; (3) pigment cells. The rod cells are elongated columnar, their long axes being at right angles to the horizontal plane of the rods of the retina. They each consist of two portions - a thin-walled lightly staining outer portion containing very finely granular protoplasm and a large nucleus with nucleolus and very apparent chromatin network - and a thick walled deeply

staining inner portion abutting on the pigment layer (2). The deep stain of the inner third of the rod cells is due to the thickness of the cell walls which take the stain much more readily than the protoplasm does.

In the second layer no cell boundaries can be made out, but the presence of a number of nuclei exactly resembling the nuclei of the epithelial portion of the ganglion indicates the cells of the second layer, for which I propose the name intermediate cells of the retina.

The third layer 3 is the pigment layer composed of cells so full of pigment granules and so closely massed together that no structure can be made out. Lately, the [illegible] and a comparison with other species shows them to resemble, save for the pigment they contain, the cells of the [illegible]

layer of the retina, or the ordinary cells of the ganglion. These pigment cells are arranged in a semicircle enclosing the intermediate cells and the inner ends of the rod cells.

I did not find the innervation of the eye in the solitary Cyclosalpa pinnata, but in the solitary Salpa democratica-mucronata the outer thin-walled ends of the rod cells receive fine fibres that come from the dorsal part of the ganglion, apparently coming out from the fine cellular core, through the thick outer cellular portion. It is probable that the eye receives fibres also directly from the dorsal cells of the ganglion.

The distinctive histological character of the retina is seen from this description to consist of but two kinds of modification of the ordinary ganglion cells: first, the pigmentation of certain cells otherwise unmodified; second

more complicated differentiation of the rod cells. No lens is ever present. The eye must be a very efficient light perceiving organ, but the arrangement of the rod cells, the total lack of ganglion, and the simple character of the whole organ seem, beyond doubt to show that it can give no perceptual image.

The Development of the Eye of Cyclosalpa pinnata, solitary form.

At a time in the development of the embryo, when the central cavity of the nervous system has just been obliterated and the [illegible] cells of the ganglion are degenerating to form the central, non cellular core, the cells destined to form the optic ridge push up from the dorsal surface of the ganglion. These cells are arranged from the first in a ridge having the characteristic horse-shoe shape, the open end of the

horse-shoe being anterior.

The ridge increases in size as the ganglion grows. As the central cells of the ganglion degenerate the cells of the core of the ridge also degenerate; the strands not being separated but being from the first continuous with each other.

At a considerably later period the retina cells begin to assume their characteristic appearance. The first noticeable change is the enlargement of the outer peripheral layer of cells over the dorsal portion of the ridge. They elongate and become columnar with their long axes dorso-ventral. In front of the rod cells there are about three times as many cells as having the character of the primary ganglion cells. About one third of these will remain unmodified to form the intermediate cells of the retina. At about this time the other two bands begin to become pigmented and ... [illegible]

take the walls of the inner third of each rodcell become thickened and so stain more deeply. The adult condition is reached by an increase in the size of the rodcells, by a greater thickening of the walls of these inner ends, by a greater deposit of pigment in the inner cells of the retina and by a shifting of the retinal area from the dorsal surface to the dorsal part of the inner surface of the ridge. Of course by this shifting the long axes of the rodcells which were originally vertical become horizontal.

The Anatomy of the Eyes of Cyclosalpa pinnata, chain form

The histological structure of the retina of the dorsal eye of the chain form of Cyclosalpa pinnata agrees closely with that of the solitary form, save that no intermediate layer of cells is present between the rods and the pigment

cells; i.e. all the cells of the retina except the rod cells have become pigmented. The shape of the eye on the other hand, differs greatly from that found in the solitary form. There are present in the chain Cyclosalpa pinnata two pairs of small eyes, till now undescribed, in addition to the well known unpaired dorsal eye.

The unpaired dorsal eye

This is situated on the dorsal surface of the ganglion, in a position similar to that occupied by the eye of the solitary form, except that it extends beyond the anterior face of the ganglion, nearly the posterior third of the eye lying upon the brain. It consists of two almost distinct portions, the larger of which may be described as a horse-shoe with the open side of the horse-shoe posterior, differing in this respect from the eye of the solitary form

which has its open side anterior. The posterior ends of the two posterior limbs are enlarged, so that the description horse-shoe shaped is not strictly applicable to this portion of the eye. The second smaller portion lies in the curve of the anterior part of the horse-shoe. It is elongated transversely, reaching from one limb of the horse-shoe to the other. It is connected to the rest of the eye only by a number of spindle-shaped cells, binding the anterior face of the second mass to the posterior part of the anterior portion of the main body of the eye. This eye like the eye of the solitary form lies immediately beneath the ectoderm in a chamber wholly shut off from the space in which the ganglion lies except for a narrow opening on the mid line in front. The optic chamber is thus a blood space connected with the blood sinus in which the brain lies.

The arrangement of the histological elements is different in different regions. In the posterior limb the rod cells are dorsal and the pigment ventral; in the anterior curved part of the eye this arrangement is nearly reversed, the pigment being on the dorsal and posterior faces, while the rods are on the ventral and anterior faces. Where these two regions meet in the antero-lateral angles of the eye, the pigment layer of the one bends toward but is not quite continuous with that of the other, the two almost meeting on the inner face of the eye. In the second smaller portion of the eye which lies in the anterior curve of the main portion, the rod cells face posteriorly, toward the open end of the horse-shoe, while the pigment layer faces anteriorly, lying close to the pigment layer of the anterior part of the main body of the dorsal eye.

The eye is innervated by two optic

nerves, that arise in the nucellular core of the ganglion. The fibres run in two bundles, one on each side, over the anterior and dorsal faces of the two posterior limbs of the eye, some of them here entering the clear ends of the rod cells. Further forward at the point where the relative position of rod cells and pigment cells is reversed, the fibres on each side divide into two bundles; one bundle going directly to the clear ends of the rod cells of the second smaller portion of the eye, the other passing around the inner side of the eye, below the secondary portion, to innervate in the same way the rod cells of the anterior portion of the eye.

The two pairs of smaller eyes.

The four smaller eyes of the [illegible] form

of Eucloszira *inermata* are arranged in two pairs; one pair lying over the posterior face of the ganglion, on each side of the middle line; the other pair lying just below the posterior ends of the two posterior limbs of the unpaired dorsal eye.
The lie imbedded in the midst of the smaller cells of the ganglion, just dorsal to the zone of origin of the nerves that arise from the brain. These eyes consist simply of rod cells which exactly resemble except in size, the rod cells of the large dorsal eye. These cells are arranged in a hemisphere, with their thin walled, lightly staining ends posterior and their thick walled, deeply staining ends toward the centre of the ganglion.
The membrane of the posterior face of the ganglion touches the posterior ends

of the rod cells. In the specimens studied all of which were hardened in acid reagents, no pigment was found in the region of these eyes. In the live Cycloralpa it may be that certain of the ganglion cells near the base of the rods are lightly pigmented; this pigmentation can not be very decided, for, if present in the specimens studied, it had been dissolved by the same reagents that had left apparently unimpaired the pigment granules in the pigment cells of the large dorsal eye.

The structure of the dorsal pair of small eyes is the same as that of the posterior pair. In this case however, the rod cells, which are arranged in a hemisphere, have their nucleated ends pointing toward the centre of the ganglion and

their thick walled ends abutting on the pigment layer of the large dorsal eye. The right one lies at the base of the right optic nerve, on the right side of and a little in front of it. The left one is situated in a corresponding position on the left side. The pigment layer of the unpaired dorsal eye is separated from the rod cells of each small, dorsal eye by the delicate neural membrane that intervenes. This may or may not prevent the small dorsal eyes functioning as light perceiving organs in connection with the pigment of the large dorsal eye. It indicates that the small dorsal eyes can not be regarded as parts of the larger unpaired eye.

The Development of the eyes of Cyclosalpa pinnata, chain form.

Dorsal unpaired eye.

The early stages of development of this eye in the chain form are almost identical with those in the solitary form. It first appears at a time when the central cells of the ganglion are commencing to degenerate. It has, from the first, the characteristic horse-shoe shape seen in the eye of the solitary Cyclosalpa. The horse-shoe shaped arrangement of the cells of the rudiment of the eye is very soon lost but it is always present for a short time. I have examined serial sections of the ganglia of more than one hundred individuals of about the age represented and have always found

the same appearance of a definite, though slightly developed, horse-shoe shaped ridge. This appearance is so constant and uniform, that we can safely say the eye of the chain Cyclosalpa passes through a stage when it corresponds in shape to the eye of both the adult and embryonic solitary Cyclosalpa pinnata. The central cells of the ganglion and the cells of the core of the ridge degenerate at the same time as is the case in the solitary Cyclosalpa.

Very soon the horse-shoe shaped arrangement of the eye cells is lost. They are, from the first, close pressed to the ectoderm. Soon after the appearance of the optic ridge the ectoderm arches up over the ganglion, carrying with it the cells of the ridge.

The eye cells loose their connection with the ganglion, except that the noncellular core of the ridge is pulled out into long fibres, that bind the eye cells to the ganglion. The rudiment of the eye is now a thickened disc of cells, close pressed to the ectoderm, with fibres connecting the centre of its ventral face with the non cellular core of the ganglion. As development proceeds the anterior edge of the disc approaches the brain till it comes in contact with it. While the anterior edge shifts its position, the posterior edge retains its former place; the disc becoming in this way nearly perpendicular to the dorsal face of the ganglion. The nerve fibres, which, from the first, connected the centre of the disc with the non

cellular core of the brain, now, of course, lie along the posterior face of the perpendicular disc. During its change of position the disc remains in connection with the ectoderm, causing the latter to approach anteriorly almost to the surface of the ganglion. The posterior edge of the disc, during this shifting of position, curls over backwards, forming the first rudiment of the second mass of retinal tissue, which lies in the anterior curve of the main body of the adult eye. The whole eye continues to bend forward till it comes to lie horizontally with the originally anterior edge of the disc posterior and the originally posterior edge anterior.

The histological differentiation of the

retinal elements, the change of form of the eye and its shifting from a perpendicular to a horizontal position, proceed simultaneously; all three processes becoming complete at the time when the circle of chain Cyclosalpae is set free from the mother stolon. As in the solitary Cyclosalpa pinnata, the rod cells are the first to distinguish themselves, appearing at the same time in all regions of the eye. Their cell boundaries become distinct. Soon they elongate becoming columnar. After a very short interval the deeper staining of their inner ends shows the cell wall of this portion to be somewhat thickened. The adult histological condition is reached by the greater elongation of the rod

cells, an increase in the size of their nuclei, a greater thickening of the cell walls of their inner ends and by a very dense deposit of pigment granules in the cells of the pigment layer of the retina. The pigmentation does not show in any of the young Cyclosalpas still attached to the stolon up to the time of the formation of the terminal wheel about to be set free. It must, then, be deposited rapidly between the time when this wheel is formed and the time when it is set free from the stolon of the solitary Cyclosalpa.

During the changes in the histological character and in the position of the eye there is a concomitant change of form. The

change from the very early horse-shoe shaped ridge on the dorsal surface of the brain to the thickened disc close pressed to the ectoderm and connected with the brain only by nerve fibres has already been noted. We have seen also that originally posterior edge of this disc curls over backwards to form the rudiment of the second portion of the eyes, seen in the anterior end of the main body of the adult eye. For a long time this rudiment is connected to the main body of the eye by a considerable mass of cells resembling the ordinary cells of the ganglion: i.e. by eye cells that still retain their primitive character. When the wheel of chain Cyclosalpae is about to close

from the stolon, this mass of cells differentiates into three portions; one forming the pigment layer of the anterior portion of the main body of the eye; another forming the pigment layer of the secondary part of the eye; the cells of the third portion becoming elongated to form the spindle cells that bind the secondary part of the eye to the main body. While the differentiation of this mass of cells in the three directions mentioned is taking place, the posterior end of the now horizontal eye is dividing longitudinally, in a vertical plane to form the two posterior limbs seen in the adult eye. Later when the young whorl is formed but is still attached to the

stolon the division is complete though the two halves of the eye are not separated by so great a space as in the adult.

While the developing eye is shifting from a perpendicular to a horizontal position, it remains attached to the ectoderm. The ectoderm is thus folded back on itself, forming the double fold seen in the adult between the eye and the ganglion.

The small paired eyes.

The two pairs of small eyes are formed at a very late period. No trace of them is found in the chain Cyclosalpa still attached to the stolon. Although their develop-ment has not been observed, they undoubtedly develop from the small

ganglion cells, in the position they occupy when fully formed. Since in those no pigment layer or intermediate layer is distinguishable, the only change in the ganglion cells necessary to produce them would be a modification of certain of these cells into rod cells, after the manner of the development of the rod cells in the large eye of the chain or solitary form.

The Anatomy of the eyes in other species of Salpidae

Cyclosalpa Chamissonis

The eyes of Cyclosalpa chamissonis are more closely related to those of Cyclosalpa pinnata than are the eyes of any of the true salpae. In the solitary form the eyes of the two are practically identical. In the chain form the dorsal eye

corresponds to the immature dorsal eye of Cyclosalpa pinnata just before the latter is set free from the stolon. It has the same position directly behind the anterior face of the ganglion, with about its anterior third lying upon the dorsal surface of the ganglion. It is noteworthy that in this species the eye has not bent quite so far forward as in the adult Cyclosalpa pinnata, but is in a position corresponding to that seen in the eye of the immature Cyclosalpa pinnata. There are seen two portions of the eye corresponding to the larger and smaller portions of the eye of Cyclosalpa pinnata. In the present species these are not so distinct as in that species, distinctly being bound together by a few slender shaped cells connecting the pigment layer of the one with that of the other; they are connected by a considerable mass of [illegible] cells.

which are pigmented and serve as the [illegible] base for both portions of the eye. There are in Cyclosalpa Chamissonis no distinct posterior limits of the eye, but this portion is an undivided, continuous structure retaining the condition found in the immature chain Cyclosalpa pinnata. The relative arrangement of the histological elements in the three regions of the eye and also the histological structure and the innervation is the same in both species; except that the rod cells are shorter in the posterior part of the eye of Cyclosalpa Chamissonis. The histological structure of the dorsal eye of the chain form of the latter species corresponds then to the condition found in the adult Cyclosalpa pinnata while the position and form of the eye corresponds to that found in the immature Cyclosalpa pinnata. The un-

paired dorsal eye of Cyclosalpa pinnata passes through a Chamissonis stage. The marked similarity in form, structure and position of this eye in the two species makes it certain that, in the course of its development the dorsal eye of the chain Cyclosalpa Chamissonis undergoes a shifting of position similar to that described for Cyclosalpa pinnata so that in each of these species the anterior end of the eye was primitively posterior and vice versa.

The two pairs of smaller eyes found in the chain form of Cyclosalpa pinnata are represented in the chain form of Cyclosalpa Chamissonis by two pairs of small eyes with the same form and structure and much the same position as in Cyclosalpa pinnata, the first pair being a little more dorsal than in the latter species.

The structure of the eye in these two species confirms the conclusion drawn from other anatomical resemblances that the two are closely related, Cyclosalpa Chamissonis being the more primitive, and that they are somewhat removed from the other Salpidae.

Salpa cylindrica

The eye of Salpa cylindrica in both the solitary and chain forms, presents more marked differences from the condition found in Cyclosalpa pinnata. In the solitary form the only point of difference is that the rod cells of the posterior curved part of the horse-shoe are directed ventralward instead of forward and the pigment layer is dorsal. In the two anterior limbs of the eye the condition is the same as in the corresponding regions of Cyclosalpa pinnata.

In the eyes of the chain form there are very marked features of difference —

in Cyclosalpa pinnata. The larger eye is on the dorsal surface of the ganglion, projecting a little but not far beyond its anterior face. There is a single large optic nerve entering the posterior part of the eye. There are two eyes: the larger, plainly seen in surface view; the other smaller, placed behind the former on the dorsal surface of the ganglion. The smaller eye corresponds to the dorsal pair of smaller eyes seen in Cyclosalpa pinnata. It agrees with the latter in histological structure and in position, only that the two have fused together in Salpa cylindrica across the middle line, behind the optic nerve. Notice that the thin-walled, nucleated ends of the rod cells of the small eye point toward the core of the brain as is the case with the rod cells of the small dorsal eyes of Cyclosalpa pinnata. The fusion of the two small dorsal eyes into one in Salpa

cylindrica corresponds to the more compact form of the larger eye and the fusion of the two optic nerves into the single nerve found in the latter species. There is no organ in Salpa cylindrica corresponding to the posterior pair of small eyes in Cyclosalpa pinnata.

In the larger eye the layer of intermediate cells is mostly wanting though a few do show here and there. In other words the posterior cells of the retina have almost all become pigmented. In this region the rod cells are seen to be dorsal and the pigment layer ventral. In the anterior region of the eye this arrangement is reversed the rod cells being ventral and anterior and the pigment dorsal. There is no secondary portion of the eye corresponding to that which lies in the anterior curved portion of the larger dorsal eye of Cyclosalpa pinnata, chain form. There are however two peculiar

small lobes of the eye. They are a structure characteristic of this species, not being developed in any other. They are not, without further study of the development, to be homologized with the smaller portion of the dorsal eye of the chain Cyclosalpa pinnata, because of the exactly opposite relative position of the histological elements in the two cases.

Salpa runcinata-fusiformis

Solitary form

In the eye of Salpa runcinata fusiformis we find quite marked variations from any of the forms described. In the solitary form we have the typical horse-shoe shaped retina in the usual position, but the development of retinal tissue at the anterior ends of the two anterior limbs is very great. In this region all the cells of the whole optic ridge are

modified to form the retina. In this species, as in Salpa cylindrica, the pigment layer of the posterior portion of the eye is dorsal; next to this comes the layer of intermediate cell; ventral to this again are the rod cells. These are not definitely columnar and arranged in a single layer, but they are irregular in shape, have irregularly thickened walls and are arranged in an agglomerate mass. The rod cells are elongated in a dorso-ventral direction, suggesting vaguely the columnar structure of the corresponding cells of the retina of Salpa cylindrica or Cyclosalpa pinnata. Further forward, in the anterior limbs of the eye, the relative position of pigment cells and rod cells is changed; the former

fering on the outer, the latter on the inner face of the optic ridge. This corresponds to the position in other species. Between the anterior limbs of the eye is a great mass of rod cells. They are best called rod cells because of their undoubted relation to the typically developed rod cells of other species, though in this species they do not have the ordinary structure of rod cells. This ventral extension of the anterior ends of the two anterior limbs of the eye is a peculiar feature, not represented in the solitary form of any other species [illegible]. The condition of the rod cells seems to indicate that the retina is degenerate, but rod cells of a very similar character are found in several species not

to be described, and it will be wise to defer any discussion of the point till we can gain a comprehensive view of all such species.

Between the ectoderm and tunic in the region above the ganglion and eye there is a large cavity which in life would be full of sea water. This would act as a cushion and must be a very efficient protection for the ganglion and eye.

Chain form.

The eye of the chain form of Salpa cunninata-fusiformis shows certain very interesting characters. In shape it is elongated ovoid, with the more pointed end anterior. Its long axis is nearly horizontal and is directed forward and about twenty degrees to the right or left.

It lies wholly in front of the ganglion; its posterior end abutting on the antero-dorsal surface of the ganglion. The relative position of the histological elements is much the same as in Salpa cylindrica. In the posterior position of the eye the rod cells are dorsal and the pigment cells ventral. In the anterior position this arrange-ment is reversed the pigment being dorsal and the rod cells ventral. The innervation is as in Salpa cylindrica. The optic nerves arise from the antero-dorsal part of the ganglion, running over the dorsal face of the posterior part of the eye, innervating the rod cells of this region; and then bores through the eye to innervate the thin walled ends of the ventrally directed

rod cells of the anterior portion. The structure of the rod cells is the same as in Cyclosalpa pinnata, or Salpa cylindrica. The pigment cells are fewer in number than in either of the latter species and are not massed together. They are branched, having an appearance as if amoeboid. They are large, with large nuclei and finely granular protoplasm in which are found a great quantity of pigment granules of different sizes. The intermediate layer of the retina is present and the cells are remarkably distinct. They are small cells with small nuclei. Their protoplasm is clear and almost homogeneous, like that of the nucleated ends of the rod cells. The most interesting feature is that they each send

up one (or more?) processes toward the rod cells. Although I have been unable to make successful macerations and can not speak with absolute certainty, still I am convinced, after careful study of serial sections, that each of these processes connects with the protoplasmic core of the thick walled end of one of the rod cells. The delicate membrane that surrounds the eye does not include the pigment cells, but intervenes between them and the intermediate cells. The pigment cells are attached, some to this membrane, and some to the basement membrane of the ectoderm, while others are attached to both. A similar, though less distinct membrane, is found between the intermediate cells and

the pigment cells in certain other species: e.g. Salpa cylindrica, solitary form, Salpa hexagona, solitary and chain forms and Salpa cordiformis-zonaria, solitary form. Also in several species, where the intermediate are not present, the rod cells are separated from the pigment by a similar membrane. Beside the larger eye there is, in the chain form of Salpa runcinata-fusiformis, a smaller collection of cells just dorsal to the point of origin of the optic nerve, which have a structure closely resembling the structure of the rods in many species. Like the rod cells of the solitary form of this species they have no regular shape, but the characteristic thickening of their cell walls is present. As

will be seen by comparison with forms yet to be described, they must be regarded as rod cells, which are either degenerate, or have not attained to the typical structure. Their position dorsal and posterior to the point of origin of the optic nerve, indicates that they are homologous with the smaller eye found in the chain Salpa cylindrica and so with the dorsal pair of small eyes found in Cyclosalpa pinnata, chain form.

Salpa africana-maxima.

The shape of the eye of the solitary form resembles that found in the solitary Salpa runcinata-fusiformis. (I have been unable to study sections of the solitary form). In histological

structure the large eye of the chain form agrees very closely with that of the chain form of the last species. There is a mass of imperfect rod cells in the inner part of the ganglion corresponding closely in shape, in position and in the character of its component cells to the similar structure found in Salpa runcinata-fusiformis. The only noticeable difference between the eyes of the two species is in the shape of the larger eye in the chain forms. In Salpa Africana-maxima this is nearly globular or strictly ovoid, while in Salpa runcinata-fusiformis it is elongated ovoid. The close resemblence between the eyes of these three species indicates the closest relationship.

Salpa hexagona

The Fish Commission collection contains no specimens of the solitary form of this species. The principal eye of the chain form much resembles the larger eye of the chain Salpa runcinata-fusiformis in shape, relative position of histological elements and innervation. The histological character of the rod cells resembles more closely that of the imperfect rod cells of the small eye of the chain Salpa runcinata-fusiformis and yet more closely that of the rod cells of the eye of the solitary form of that species. The rod cells are roughly cylindrical, with irregularly thickened walls. They are not arranged in a single definite layer, but are somewhat irregularly disposed.

The rod cells and intermediate cells are enclosed in a very delicate membrane. Outside this membrane, ventral to the intermediate cells, between them and the ectodermal optic sheath are the pigment cells, resembling the pigment cells of Salpa runcinata-fusiformis, chain form. They are irregular in shape; their protoplasm is so full of pigment granules that their nuclei can be seen only after dissolving the pigment in acid.

In the chain form of Salpa hexagona there is a pair of dorso-lateral outgrowths from the ganglion, one on the right side, the other on the left side of its dorsal face. These are spherical and composed of polyhedral cells with thick walls and large nuclei

of the size of the large nuclei found in the periphery of the ganglion, or in the rod cells of the dorsal eye. The character and homology of these outgrowths can best be discussed after describing a simpler form of what I regard as the same organs in Salpa scutigera-confederata. I will now call attention only to the fact that their position, on the dorsal surface behind the optic nerve, corresponds to the position of the smaller eye of the chain Salpa cylindrica or Salpa runcinata-fusiformis, and the character of the cells of the outgrowths resembles that of the imperfect rod cells of the smaller eye of the latter species.

Professor Brooks has called my attention to a peculiar structure in the young

embryo of Salpa hexagona. It is seen in the embryo at a time when the ganglion is well formed but has not yet attained the compact structure seen in the latest stages: the central cells of the ganglion have not yet commenced to degenerate nor has the eye appeared. The ganglion lies close to the dorsal ectoderm. Near the posterior end of the ganglion there is a wide and deep invagination of the ectoderm running obliquely downward and backward toward the dorsal wall of the stoma. The walls of the invagination are pressed together so that the whole structure appears to be merely a double fold of ectoderm with no lumen between. The double fold of ectoderm is crescent-shaped, the

horns of the crescent projecting forward on each side of the ganglion a little beyond its middle point. It is wider than the ganglion and a little longer antero-posteriorly. In histological character the cells of the invagination resemble the ectodermal epithelium. This structure arises as a mere pit in the ectoderm following the lateral and posterior boundaries of the ganglion. In the earliest stages, when the ganglion is just commencing to enlarge, the dorsal ectoderm is an even surface. As the ganglion grows, it pushes the ectoderm upward, forming a rounded hillock. In later stages of development the ectodermal epithelium still clings to the whole dorsal surface of the

invagination. That portion of the ectoderm behind the brain, however, grows rapidly and pushes up over the brain, overlapping from behind forward the epithelial covering of the brain. In this way there is formed the double fold of ectoderm described. It arises then, not as a direct invagination, but by an over growth. I do not know its fate since I have had no opportunity to study the later stages of development or the adult of the solitary form. I am unable to see that this structure has any important morphological or physiological significance. It does not seem to be worthy of the name organ, though possibly, if present in the adult, it may serve as a slight protection for the

ganglion.

Salpa costata - Tilesii

In the chain form of this species, which shows a still less definite structure of the rod cells in the larger eye, there are indicated structures which I regard as probably homologous, one with the dorsal pair, the other with the posterior pair of smaller eyes of Cyclosalpa pinnata, chain form. In the large eye is seen an irregular mass of rod cells which show no indication of the typical structure except in the thickening of their walls. They are irregularly polyhedral in form and are not noticeably elongated. There is but slight indication of two regions of the eye, corresponding to the two

regions in the large eye of the chain form of Salpa runcinata-fusiformis. Such indication as there is is given by the arrangement of the pigment cells. There is a single, continuous layer of these between the mass of rod cells and the ecto-derm of the optic sheath. This layer is, however, thicker and more dense in two regions, one on the ventral face of the eye near the ganglion, the other on the dorsal face near the apex. The positions of these more developed portions of the pigment layer correspond to the positions occupied by the two masses of pigment cells in the two regions of the larger eye in the chain forms of Salpa hexagona, Salpa runcinata-fusiformis and other species. In this way we have a slight, but decisive,

indication of the division of this eye into two regions which, when typically developed, show the structure found in the larger eye of the chain form of Salpa runcinata-fusiformis.
In the posterior face of the ganglion there is another large mass of irregularly polyhedral cells with thickened cell walls, closely resembling the rod cells of the dorsal eye. What may be the meaning of these cells I am unable to say with certainty. The cells much resemble the rod cells of the large dorsal eye of the same species: the posterior pair of eyes in the chain Cyclosalpa pinnata, though much smaller occupy about the same position. The pigment spots in the ganglion of Pyrosoma are in a position corre-

sponding to the ventral portion of this mass of cells. I think it very probable that this structure is homologically an eye, having the same relation to the posterior pair of small eyes found in Cyclosalpa pinnata that the large dorsal eye of Salpa costata-Tilesii bears to the unpaired eye of the former species. On the opposite side of the ganglion beneath the dorsal eye and in front of the optic nerve there is still another mass of similar, imperfect rod cells, and in close connection with them, a patch of deeply pigmented cells. Neither the rod cells or the pigment cells show so well in the section figured as in the adjacent sections. The structure of this mass of cells and its position, comparable to the position of the dorsal pair of small eyes in the chain form

of Cyclosalpa pinnata, indicates that it is homologous with these eyes in the latter species. The presence of pigment in connection with this structure in Salpa costata-Tilesii is a variation which confirms the view that it is a light perceiving organ, though the typical histological character of the rod cells is not found.

We come now to quite a distinct group of Salpas, including Salpa scutigera-confederata and another species, or more probably variety, not recognised by Traustedt, which is probably the Salpa bicaudata of Salensky and various authors.

Salpa scutigera-confederata

I have not been able to section the

eye of the solitary form of this species, for the Fish Commission collection included but one specimen. In surface view the eye exactly resembles that of the solitary Cyclosalpa pinnata, i.e. it is typical.

The dorsal eye in the chain form shows two well marked regions, in one of which (the anterior) the pigment is dorsal and the rod cells ventral, while in the other (the posterior) this arrangement is reversed. The rod cells are of the same character as those of the larger eye of the chain Salpa costata-tilesii. The pigment cells are so massed together and so full of pigment that no structure can be made out. The optic nerve arises from the dorsal part of the ganglion

and enters the eye between the pigment layer of the posterior region and the rod cells of the anterior region. No intermediate cell-layer can be distinguished. The greater share of each region of the eye (all save the pigment layer) is composed of thick walled, polyhedral cells like those in Salpa costata-Tilesii chain form. The comparative thickness of the cell walls is greater however, in Salpa scutigera-confederata.

Two masses of similar, thick walled cells are present in the ganglion, one on the right, the other on the left, a little above the mid point of the lateral faces of the ganglion. These cells exactly resemble the peculiar rod cells of the large dorsal eye in size, shape, charact-

of nuclei, thickness of cell walls, in manner of staining, and in their general appearance. The arrangement of the chromatin in their nuclei and in the nuclei of the rod cells of the dorsal eye is very different from that seen in the other cells of similar size found in the periphery of the ganglion. In the former the nuclei contain many small chromatin granules and no very large nucleolus. The other cells of the ganglion are of two sorts, the one sort small with small nuclei. These are utterly different from the cells we are discussing. The other kind of ganglion cells are larger, about equal in size to the rod cells of the eye. They have the same sized nuclei, but in these the chromatin is nearly all collected into a large nucleolus, giving a

decidedly different appearance from the nuclei of the rod cells. Besides this their protoplasm reacts much more strongly with haematoxylin, giving a deep stain, while the protoplasm of the rod cells stains very weakly. These characters and especially the great thickness of their cell walls distinguish the rod cells of the eye and the two lateral masses in the ganglion from any other of the nerve cells. We must, then, regard these two lateral masses of rod-like cells that are found in the ganglion as imperfect or degenerate eyes bearing the same relation to the larger eye of this species as the smaller dorsal eyes of the chain Cyclosalpa pinnata do to the large unpaired eye of that species. These structures just described form

a connecting link between the smaller eyes found in Cyclosalpa pinnata and Salpa cylindrica, which are undoubted optic organs, and other structures found in Salpa hexagona, Salpa costata-Tilesii and Salpa coriformis-zonaria, which are so different from the typical eye that one would not readily recognise their true character. These structures can not function as optic organs and when I apply to them the word eye I mean merely that they are homologous to structures in other species that are undoubted eyes and that the same sort of histological modification which has produced them from the cells of the ganglion has produced the rod cells of the larger dorsal eye of Salpa scutigera-confoederata.

The manner of innervation of the dorsal eye of Salpa scutigera-confederata is very suggestive when compared with that of the corresponding eye in the species thus far described. In this species the optic nerve passes up from the ganglion and enters the eye at its mid-ventral point. This reminds one strongly of the condition in a very young chain Cyclosalpa pinnata, where the eye has the form of a thickened disc close pressed to the ectoderm and the fibres of the optic nerve bind the centre of its ventral face to the dorsal part of the ganglion. This primitive condition which has been retain in Salpa scutigera-confederata has been altered in Cyclosalpa pinnata owing to the reversal that takes place during the

development of its eye, in which the originally anterior edge of the optic disc becomes posterior and its originally ventral surface dorsal. In this way, in Cyclosalpa pinnata the optic nerve came to lie on the dorsal surface of the posterior part of the adult eye. The manner of innervation of the dorsal eye of the chain Cyclosalpa Chamissonis, Salpa cylindrica, Salpa runcinata-fusiformis, Salpa Africana-maxima, Salpa costata-Tilesii agrees closely with that found in the chain Cyclosalpa pinnata. This can be explained only by the supposition that in all these species there has occurred a shifting during the development of the eye, comparable to that described for Cyclosalpa pinnata. The innervation

two lobes representing the two regions seen in the dorsal eye of the chain Salpa scutigera-confoederata. There is seen the same contrast in the relative position of the pigment layer and the rod cells in the two lobes as in the two regions of the eye of the last species. The two lobes of the eye are not, however, anterior and posterior, as we should expect. A twisting through an arc of forty-five degrees has taken place, by which they are brought to lie in a direction oblique to the long axis of the body. The innervation of the eye is the same as in the last species; except that the optic nerve forms a long stalk by which the eye is elevated above the ganglion. In Salpa bicaudata there are no smaller eyes nor any indication of structures homologous to them.

Above the eye in the chain form of this species there is a great thickening of the tunic, forming a cushion or pad, that must be a very effective protection for the eye and ganglion.

Salpa democratica-mucronata

In Salpa democratica-mucronata we have decided points of difference from any other species. The eye of the solitary form closely resembles that of Salpa cylindrica. The chief point of difference is that in the former there are no intermediate cells of the retina to be distinguished.

In the chain form of all other species the the larger eye is situated on the dorsal or antero-dorsal face of the ganglion. The form and structure of the eye and the arrangement of the ectodermal optic sheath show

that in Salpa democratica-mucronata there has been a shifting of the whole ganglion, by which the originally dorsal face bearing the eye has become antero-ventral. The eye then arises from what was originally the dorsal face of the ganglion. The Ecto[illegible] has remained attached to the originally dorsal and anterior faces of the ganglion, as it is in other species, so, in the shifting of the ganglion, it has been carried ventralward making a loop beneath the ganglion.

The eye is divided into three portions. In the anterior of these the rodlets are on the side toward the ganglion, i.e. are dorsal, and the pigment layer is next the ectoderm, i.e. away from the centre of the ganglion, or ventral. In the [illegible] [illegible] portions [illegible] point away from the ganglion, i.e. are ventral.

The optic nerve enters the eye between the three regions and is distributed directly to their rodcells. There is in Salpa democratica-mucronata no portion of the eye homologous to the median portion of the large eye of the chain Salpa cylindrica or Cyclosalpa pinnata. These homologies are deduced from three points, first the [illegible] which has taken place in the ganglion of Salpa democratica-mucronata; second, the relative position of the histological elements in the different portions of the eye, and the relation of this position to the three principal axes of the ganglion; third, the innervation of the eye.

We see then that Salpa democratica-mucronata falls into the same group with Salpa cylindrica [illegible]

formis, Salpa africana-maxima, Salpa [illegible] and that in this species, as in [illegible] occurred a shifting of the developing eye of the chain form, that has caused the originally ventral surface to become dorsal, as [illegible] of the chain Cyclosalpa pinnata [illegible] shown by the innervation [illegible] in the development [illegible] the members of the group just mentioned.

Salpa cordiformis-zonaria

This species [illegible] features in the eye of both the chain and solitary forms. The eye of the solitary form agrees in histological character with the eye of [illegible] pinnata or Salpa cylindrica; i.e. it has the typical histological

structure. In shape, however, it shows a divergence from the eyes of all other species. The anterior ends of the horse-shoe shaped eye project outward and obliquely to the right and left. Only the [illegible] ganglion. Although the shape is different from that of the typical eye of the solitary forms, it is really but a slight modification of that eye. It is important however as the only considerable modification shown in the shape of the eye of the solitary [illegible].

In the chain form the eye has the typical position on the dorsal face of the ganglion. It is oval in shape, with its long axis a little inclined to the long axis of the body.

a study of the histological structure and the arrangement of the histological elements shows that here again we have represented, in a disguised form, the anterior and posterior regions of the eye, corresponding to the similar regions found in the three eyes of the other type [illegible] and [illegible]. The rod cells of the [illegible] basal portion are seen to connect directly with the fibers of the optic nerve. The eye of this species is very compact; the apical portion being brought back under the basal portion, so that the thick walled ends of the rod cells of one region are in close connection with the thinner walled ends of the rod cells of the other region.

In figure 13 we see the [illegible] of the foveal portion. In a section exactly in the mid line of the eye we would see that the [illegible] of the eye does not there approach so far toward the base of the eye and that beneath the rod cells of the [illegible] region are pigment cells like those seen in the section drawn. This eye then in spite of its consid- erable modification still conforms to the general type: and its manner of [illegible], would seem [illegible] that [illegible] in the larger eye of the chain [illegible] [illegible], [illegible] that in this species [illegible] we have a [illegible] of [illegible] in the [illegible] eye. The rod cells are columnar, with their outer nucleated

cells stain easily and the cell walls of their inner ends unevenly thickened.

It may seem that possibly the irregular shape of the rod cells seen in the sections of the eyes of the same individuals of certain species, e.g. Salpa hexagona, Salpa costata-Tilesii, Salpa cordiformis-zonaria, is due to the cells being cut obliquely. I would say that I have cut sections of each eye in three planes and find the same irregularity of shape in all.

I realize the incompleteness of the histological observations given in the preceding pages. I am not however able to make them more complete until I am enabled to obtain fresh material by maceration methods, the

use of which is so essential for gaining a right understanding of the shape of the cellular elements and especially of the manner of innervation. I hope at some future date to make a more complete contribution to the knowledge of the histological elements of the nervous system and eye of Salpa.

General Part.

We have seen in the foregoing descriptions that the eye of the solitary form has a very uniform structure throughout the different species, the condition in Salpa [illegible] being probably typical. There are but two noteworthy variations; the first is the remarkable [illegible]

[illegible] seen in [illegible] [illegible]-fusiformis; the second is the slight [illegible] from the [illegible] [illegible] [illegible] in [illegible] cordiformis-Zoaria.

We have also seen that the eye of the [illegible] passes through a stage in its development when it resembles the eye of the [illegible] form. This is observed even in the group with the most modified eye, the [illegible].

In the adult forms of the different species there is a very great degree of variation in the structure of the eyes. Yet it is not difficult to see, in all, distinct indications of the same fundamental plan, which [illegible] most exemplified in the

chain Salpa runcinata-fusiformis. The variation affects the number, position, size, shape and histological character of the eyes; and so universal is the variation, that the eyes of no two species are alike. Salpa runcinata-fusiformis and Salpa hexagona-maxima most closely resemble each other, but even between these species there are differences in the shape of the large eye, the size of the optic chamber, and the shape of the intermediate and pigment cells.

This so great and so prevalent variation in the eyes of the several species which all conform more or less closely to the same fundamental type, offers an especially favorable

opportunity for studying the relation-
ship between species. If the variation
had been so great that the uniformity
to the type were lost in the adult,
a careful embryological study of the
eye would be necessary to throw much
light upon the relationship; but
since in the adult forms we have
present both the variation and the
fundamental uniformity we can
safely deduce certain evidence as to
the relationship from a comparative
anatomical study. This in connect-
ion with a careful study of the
development of the most highly
specialized eye (that of Cyclosalpa
pinnata) gives us good data
from which to gain evidence as
to the development of the different species

of Salpidae. The history of a single important organ, which we have in this way obtained can be reasonably taken as a source of definite and important evidence as to phylogeny; though of course it is only evidence and can not be taken as decisive proof. A similar study of all the organs would be necessary to fully establish the phylogenetic relations between the species.

In Salpa we see especially shown, since in the solitary form we have a conservative member, while in the chain form we have a more modified member of the species. It is as if an animal were placed in such peculiar conditions that one portion of its body should retain primitive characters while another portion of its body should undergo the most decided changes. In Salpa the divergent member (chain individual) is so removed from the more

conservative member (the solitary Salpa) that its modification has unusually little affected these other features of the conservative member. The modifications of the chain form in structure, however, has bearing upon phylogenetic conclusions. Those of the eye also affected the solitary form of the species, variations in the chain form and variations in the solitary form all come from the same ultimate source, in general those produced by the solitary [illegible].

What relationships between species does the evidence from the eyes favor? The fundamental conformity of plan in the eyes of the different species shows what is universally recognized, namely, a common ancestry. Again — in certain instances, the closest agreement in structure between the eyes of two or more species, indicating a natural group. Cyclosalpa pinnata and Cyclo-

-alpa chamissonis form one such quite distinct group. The eye of the chain Cyclosalpa pinnata passes through a chamissonis stage, indicating that the latter species is the more primitive of the two. Again the almost perfect uniformity of structure in the eyes of Salpa runcinata-fusiformis and Salpa africana-maxima indicates that these form a natural group. But the fact that the manner of innervation of the large dorsal eye of the chain form of these species points to a reversal of position during the development, similar to that described for Cyclosalpa pinnata, indicates that these two Salpas fall into a larger natural group with the Cyclosalpas. This group includes also the other Salpas in which a similar reversal of the position of the large horseshoe eye occurs; i.e. Salpa cylindrica, Salpa hexagona, Salpa costata-Tilesii, Salpa cordi-

fusiformis, Salpa democratica-mucronata, quite distinct from the large group and the natural group including Salpa scutigera-confoederata and Salpa [illegible], [illegible] also [illegible] of the type [illegible] above. This is shown by the manner of innervation. The larval eye of the chain Cyclosalpa pinnata passes through a stage when in shape, position and innervation it resembles the adult eye of the chain Salpa scutigera-confoederata; so it is safe to say, so far as the evidence from the study of the eye goes, that the group including the latter species is more primitive than the large group in which we find Cyclosalpa pinnata and Salpa runcinata-fusiformis.

Between the members of the larger group we find varying degrees of resemblance in the eye. Salpa cylindrica stands about midway in the group. Salpa democratica-mucronata

shows the greatest divergence from this species. Salpa runcinata-fusiformis and Salpa Africana-maxima agree quite closely with it. Salpa cordiformis-zonaria stands next far removed. The Cyclosalpa form a quite distinct group with a more highly specialized system unlike cylindrica and bearing a close relation to that of the latter. Salpa costata-Tilesii shows resemblances to each of the members of the cylindrica group and at the same time shows striking differences from each. It is hard to see to which it is most closely related in the structure of its eye though in the position of its smaller eyes it most nearly approaches the Cyclosalpa.

What is the fundamental plan of the eye of Salpa?

The eye is formed from the central nervous system and not directly from the ectoderm

conforming in this respect to the Vertebrate rather than the Invertebrate type. It is a simple eye readily comparable in structure to the pineal or "parietal" eye of Vertebrates. It is composed of a series of optic units, each of which consists of a rod cell and one or more pigment cells. That end of the rod cell which receives the innervating fibre is thin walled and contains the nucleus. The other end of the rod cell which is near the pigment cells, is thick walled resembling the thick walled ends of the Vertebrate rod and cone cells. The rod cells the essential element in each are alike and the innervation is the same. The optic unit of the Vertebrate eye is more complex than that of Salpa, having certain ganglion cells interpolated between

the rod cells and the brain; but the fundamental character of the two is the same. The eye in the two groups is formed by a similar modification of the cells of the central nervous system. This modification having gone further in the Vertebrate than in Salpa. Although the eye of Salpa so closely resembles the Vertebrate eye in structure, it can not be regarded as homologous with the latter. It has often been homologized with the Ascidian larval eye and the Vertebrate pineal eye but such an homology can not be sustained, as we will see after we have studied the relation of the Ascidian nervous system to that of Salpa. This will

be taken up in connection with the study of the sub-neural gland.

We have in the Chordata a series of variations in the structure of the optic organs. Salpa eye falls into this series although it is not homologous to the optic organs of any other Chordata. In Amphioxus we find merely a slight pigmentation of the inner ends of certain cells in the anterior part of the neural canal. In the larval Ascidian we find a number of cells in a corresponding position, whose inner end abut on a mass of pigment. These cells are slightly evaginated and in the hollow of the evagination there are one or more

"lenses", each of which has been formed by the migration of one of the neural cells into the hollow of the optic evagination. In the Vertebrate pineal eye we have this evagination carried much further and the lens formed in a different way but the rod cells correspond to those of the larval Ascidian eye in their relation to the neural canal, their pigmented ends being toward the cavity of the neural tube. Salpa eye forms a connecting link in structure between the larval Ascidian eye and the Vertebrate pineal eye and though it is formed in a different way from a different part of the brain and forms no part of the phylogenetic series, still it

indicates a probable phase in the structural development of both the pineal and lateral eye of Vertebrates.

In the optic unit of certain species of Salpa we find a cell interposed between the rod cells and the pigment cells. I refer to the intermediate cells as I have called them. These cells are not constant, being present in some species and absent in others, and in certain species being present in the solitary form and absent in the chain form. I do not think this can be regarded in every case where present, as simply certain of the cells of the pigment layer which have not become

pigmented - In one case this may be the explanation but in Salpa runcinata-fusiformis they are separated from the pigment layer by the definite membrane which encloses the rod cells, and also they send up processes toward the rod cells, which appear to connect with the protoplasmic core of the thickened ends of the rod cells. What may be the meaning or function of these cells I am unable to say.

The variation found in the eyes of Salpidae is itself an interesting feature. The fact that this variation is slight in the solitary form while it is very great in the chain forms is an important fact.

So far as we know, there is nothing in the conditions of life of the chain form which would create a greater need for eyes of diverse structure, than is found in the solitary form. It may be that there is less rigorous selection of optic organs in the chain individuals, owing to the interdependence and mutual assistance of the members of the community.
We have noticed the great variety of shape, position and histological structure shown in the larger eye of the chain individuals of different species. An even more remarkable series of variations is shown in the smaller eyes. In some species, e.g. Salpa cylindrica, Cyclosalpa pinnata,

these show the normal optic structure. In other species, e.g. Salpa hexagona, Salpa scutigera confederata, they bear no resemblance to eyes. Yet the gradations between the two conditions, shown in other species, e.g. Salpa runcinata-fusiformis and Salpa costata-Tilesii, seem to prove beyond question that all these structures are homologous. Because of this homology I have called them all eyes, not meaning that they all function as visual organs. What is the meaning of the great diversity of structure I am unable to say. If it were not for the embryological evidence to the contrary we would seem to be dealing with a series of degeneration. If this be so I am unable to conceive

what change in the life conditions of the chain individuals have caused them to have less need of numerous well developed sight organs than formerly. It is useless to speculate upon the matter.

We have seen that in the most primitive form of Salpa eye (that found in the solitary individual) the thick-walled ends of the rod cells and the pigment layer are normally toward the brain, or, what is essentially the same thing, toward the core of the optic ridge), while their innervated ends are near the surface. The light then traverses the whole length of the rod cells before reaching the pigment; this eye is therefore "inverted." In the eye of the

solitary form of Cyclosalpa pinnata, a secondary shifting of the retina has taken place by which it is changed from the dorsal to the inner surface of the optic ridge. In the solitary form of other species the same process is carried still further till the thin walled ends of the rod cells lie toward the brain and their thick walled ends and the pigment layer lie just beneath the ectoderm. In these species the eye of the solitary form is therefore secondarily non inverted. This change from the inverted to the non inverted condition, shown in the ontogeny is probably of phylogenetic significance. In the ontogeny of the eye of the chain form we see a similar change

affected in a somewhat more complicated manner. While the developing eye of the chain Cyclosalpa pinnata is still a disc of cells appressed to the ectoderm and connected to the brain only by the nerve fibres entering its mid ventral point, we can distinguish the three regions of the eye and can determine the position of the as yet imperfectly developed histological elements. In the first region the rod cells lie next to the brain and the pigment layer next to the ectoderm. This region of the retina is therefore non inverted. In the second region the rod cells lie next to the ectoderm and the pigment layer toward the brain - this portion of the retina is

therefore inverted. In the later reversal of the eye the relation of the whole retina to the ectoderm (i.e. to the morphologically exterior surface of the body) remains the same. The relation to the direction of the light is, however exactly reversed, the first region which was at first uninverted becomes physiologically inverted; the second region, which was at first inverted becomes physiologically non inverted. The changes in the third region of the retina are still more complicated. Primitively it formed a portion of the second region and its histological elements had the same arrangement i.e. were inverted. Later when this third portion of the retina curled

over backwards, revolving through an angle of 180° it became secondarily uninverted. By the final reversal in the position of the whole eye this third region became again physiologically inverted. It is not easy to conceive the advantage derived from this complicated series of changes. One thing though seems to be most clearly indicated namely, that there is no fundamental difference between inverted and non-inverted eyes and that one sort can very readily and apparently for slight reason pass into the other sort. It is therefore to be expected that closely related animals may possess eyes differing in this regard.

A further comparison of the horse-shoe shaped eye of the solitary form with the immature eye of the chain individual should be made. That the two eyes are fundamentally similar is shown by the fact that the eye of the chain individual passes through a horse-shoe shaped ontogenetic stage. After it has assumed its disc-like form and before it has become inverted its posterior portion corresponds to the posterior curved part of the horse-shoe eye, and its anterior portion to the two anterior limbs of the horse-shoe. The primitive condition for the horse-shoe eye is that of inversion (as shown above); secondarily it becomes non-inverted.

In the immature disc-like eye of the change individual the posterior portion has an inverted retina, i.e. is primitive in this respect, since the retina in the anterior portion is from the first non-inverted. That is the ontogenetic development of the second region of the eye retains more of the phylogenetic history than does the first region of the retina. We must explain this as a coenogenetic abbreviation of the ontogeny

Section II The Innervation of the Ciliated Funnel.

The question of the innervation of the ciliated funnel in the Ascidians has been much discussed, but its actual innervation has never been shown. The nerve supply of the funnel in Pyrosoma, Doliolum and Salpa has not, so far as I can learn been demonstrated. The fact of a definite nerve supply is essential to show that it functions as a sense organ, a belief held by many of those who have worked upon the group. To establish this point, if true, one should study the living Salpa, making physiological tests. One should also make careful dissections of macerated specimens. I have been unable to secure such material and so could not study the innervation of the funnel in this way. I was able, however, to make out from a study of the stained specimens

some points that indicate a definite nerve supply. The funnel and adjacent parts were removed from specimens that had been hardened in Perenyi's fluid and preserved in alcohol; the portion removed was mounted in a mixture of glycerine and acetic acid, strongly colored with methyl green. This brought out clearly the nerve fibres, cell outlines and nuclei. In the chain form of Cyclosalpa pinnata, on the dorsal surface of the walls of the ciliated funnel, there is seen, in its [illegible] highly developed plexus of branching nerve cells and fibres. The plexus is closer, smaller meshed, over the posterior portion of the funnel, containing in this region more nerve cells and fibres than are found further anterior. A pair of strong nerves run forward from the brain into the ciliated funnel and beyond it. These nerves pass directly through the plexus and were seen in one or two cases apparently to give

of the fine branches to the plexus. The actual branching of the nerves was not seen in sections for the nerve branches are so small as to be traced with difficulty in serial sections, and the exceedingly fine branches would be impossible to find. The most careful focussing with high power [1735 diameters] indicated that the appearance seen was an actual branching and not the superposition of the nerve on the fine fibre or vice versa.

In the other forms [illegible] [illegible]-zonaria a similar though less developed plexus is found over the posterior part of the dorsal surface. Two pairs of nerves, the outer pair large, the other pair small, run forward from the brain toward the funnel. The outer pair pass over the plexus and beyond the funnel, toward the mouth. The inner, smaller pair can be traced to the funnel and along the [illegible] of the [illegible]

over its dorsal surface, then disappearing. It seems probable that these nerves connect with the nerve plexus dorsal to the funnel, though the opacity of the ciliated funnel, in this species, rendered the region so difficult to observe, that any actual connection was not made out. If there be such a connection, the whole structure may be regarded as an apparatus for the innervation of the ciliated funnel. The pair of small nerves seen in Salpa cordiformis-zonaria correspond probably to those fibres that leave the single pair of small nerves found in Cyclosalpa pinnata and join the plexus above the funnel. In other species of Salpa these organs ~~or nerves~~ are represented to different degrees. Lahille has shown that a plexus of nerve cells and fibres is present over the pharynx wall and connects the sensory cells of the lips. This manner of

immunation than is exceptional or
value

Section II. The Anatomy and Embryology of the Sub-neural Gland in Salpidae, with incidental remarks upon the homology of the nervous system in different groups of Tunicates.

As far as I can learn, the ciliated funnel is the only organ in Salpa that has been regarded up to the present time as homologous with any portion of the subneural gland of Ascidians. This has been universally regarded as homologous with the ciliated funnel of Ascidians, which serves in most species as the orifice of the excretory duct from the gland proper, and which in some species are numerous [illegible] [illegible] in Salpa certain other structures that I regard as homologous with other portions of the sub-neural gland of Ascidians, Pyrosoma and Doliolum. Before entering on the description of the

condition in the adult Salpes of different species I wish to review briefly the conditions found in the other groups of the Tunicates and then to take up the development of these organs in Cyclosalpa pinnata. After this a description of the gland in other species of Salpa will be more intelligable. With this foundation we will then be able to discuss briefly the homology of the structures described in the different groups.

Among the Ascidians Clavelina, Amaroecium, Phallusia mammillata and Molgula ampulloides will serve as examples. In Clavelina the ciliated funnel opens backward into a canal that lies upon the ventral surface of the brain, between the brain and the well developed sub neural gland. This latter is traversed by small ramifying canals that run inward into

the large canal which is the duct of the gland. The duct and the small canals that run through the gland are lined by cubical epithelium. At the level of the anterior end of the ganglion this passes abruptly into the columnar ciliated epithelium of the funnel. At the line of demarcation between the two kinds of epithelium the dorsal wall of the duct is wanting and the surface of the ganglion here bounds the lumen of the duct.

In the adult Amaroucium the conditions are somewhat different. The duct is absent, the gland and ganglion coming into close contact: but the funnel is present and its posterior portion sinks between the front portions of the gland and ganglion. It opens freely to the former by a narrow opening, but there

are no definite canals running through the ~~ganglion~~ gland and leading to the funnel. This is an indication of degeneration. The gland itself is segmented; its walls having something the appearance of the vacuolated notochord cells in the chick embryo. The chief points of difference from the gland of Clavelina shown by the gland of Amaroecium are ~~first~~ the degenerate condition of the gland (2) the absence of any duct opening into the funnel, (3) the consequent absence of any canals running from the gland into such a duct, (4) the fact that the surface of the ganglion does not at any time lie next to the lumen of the funnel, the single portion lining of the funnel lying toward the gland.

In the larval Amaroecium the duct of the gland is represented by a

posterior prolongation of the funnel; that completely separates the gland and ganglion, reaching beyond their posterior limits. At one spot on the ventral wall of the duct and at an opposite point on its dorsal wall the epithelial lining is absent; the surface of the gland and ganglion at these points reaching the lumen of the duct. There are no canals running through the gland. The presence in the larval Amaroecium of a duct of the sub-neural gland and of a communication between the ganglion and the duct show that the absence of these features in the adult Amaroecium is due to degeneration.

In Phallusia mammillata Julin discovered certain other structures which throw great light upon certain organs in Salpa I shall soon describe. The condition

of the ganglion and duct is practically the same as in Clavelina, but in addition to the small canals which open from the gland into the duct there are many lateral canals connecting the duct with the peribranchial chamber. Herdman found an important variation in two specimens of Phallusia mammillata which he examined. In these two individuals the communication of the gland with the ciliated funnel had been lost and the secretion of the gland would seem to pass out through the lateral communications with the peribranchial chamber.

In [illegible] [illegible] [illegible] found the duct enlarged into two lateral chambers which are significant in this connection.

In Pyrosoma the [illegible] [illegible]

backward into a thin-walled canal that has outlet to the ganglion close forward to its ventral surface. Seeliger and also [illegible] figure a ventral evagination of the duct with thicker walls than the rest that seems to be homologous with the [illegible] gland.

In Doliolum, according to Uljanin, we find on the antero-ventral side of the ganglion a wart-like solid process of nerve cells, connected by a small hollow tube with a [illegible] [illegible] ciliated funnel. In the young Doliolum the wart-like process from the ganglion contains a cavity of considerable size, which is continuous with the lumen of the funnel through the hollow tube. The cells of the tube in the young individuals resemble the ganglion cells, but during the growth of the animal the tube elongates and as its cells do not increase correspondingly in

number, they are drawn out into flat pavement cells forming a thin, interrupted epithelial wall around the slight central cavity of the tube. The basement membrane is continuous over the tube & the ganglion, forming the basement membrane for the epithelium cells of the walls of the tube.

[illegible] points in the development of the subneural gland and its duct in the Ascidians Phallusia and Doliolum that are of importance in connection with these organs in Salpa. In Phallusia and Doliolum these organs are at first merely the anterior opening of the canal of the central nervous system into the pharynx. In Doliolum the posterior portion of this canal is obliterated, but a portion of it persists till a late period in the cord-like [illegible] [illegible] from the ganglion.

The canal with its walls is represented in the adult by the nerves from the ganglion, the ciliated funnel and the hollow tube connecting them.

The canal of the central nervous system of the embryo Pyrosoma [illegible] freely to the exterior. This canal and its walls are represented in the adult by the ciliated funnel and its posterior prolongation that lies along the ventral surface of the ganglion, the ganglion being a secondary formation derived from the dorsal cells of the posterior part of the canal of the central nervous system. It arises [illegible] comparatively late derived by the proliferation of the cells of this region.

In the Ascidians the early relation of the ciliated funnel and the duct that runs into it to the nervous system —

difficult to determine, because of the contradictory statements of those who have studied these organisms in the group. Kowalevsky and others say the canal of the central nervous system at an early stage opens into the pharynx. From analogy with Amphioxus, Distaplia and Salpa this would be what we would expect. Van Beneden and Julin however deny the presence of such an opening, saying that the anterior diverticulum of the ciliated funnel, which becomes the duct of the subneural gland does not communicate with the canal of the central nervous system. According to these and other recent investigators the canal of the central nervous system in the larval Ascidians is wholly distinct from the ciliated funnel. The nervous system is divided into three regions.

An anterior sense vesicle which [illegible]

in the latter [illegible]; (2) a median portion from whose ventral cells the gland develops, while its dorsal cells give rise later to the adult ganglion; (3) a caudal portion which degenerates completely; in the latter case [illegible] the posterior [illegible] of the [illegible] which is shown in the earlier stages, elongates considerably, passing between the ganglion and gland and becomes the efferent duct of the gland.

It is difficult to form a definite opinion whether in the early ancestors of the Tunicates the canal of the [illegible] nervous system opened to the pharynx and this connection was lost in the larval Ascidian, or one perhaps of the most [illegible] of the authors [illegible]: or whether the [illegible]

separately from the nervous system, as some claim it now does in the Ascidians, and a communication between the two was secondarily established. If the former hypothesis is the true one, [illegible] [illegible] and [illegible] [illegible], which have retained the primitive condition which the Ascidian larva has lost. If the latter hypothesis is correct, the [illegible] appearance of the communication between the cavity of the central nervous system and the pharynx is an instance of accelerated development.

[illegible] we turn to the other [illegible] of the chain [illegible] [illegible] [illegible] and [illegible] the development of the subneural gland and the organs connected with it. We are [illegible] stage of the development of the nervous system, long before any trace of the eye

spheres, the cavity of the vesicle and the lumen of the funnel open freely into each other by a wide duct so short and wide as to hardly deserve the name duct. There is no distinction in histological character between the cells of the funnel, duct and brain, nor is there any indication, either in the thickness of the walls, or any other feature, of the boundaries between the funnel, duct and brain. The ventral wall of the posterior part of the neural canal becomes thickened. This thickening, as will be shown later, is the thick ventral wall of the "neural portion of the central [illegible] nervous system is the portion which gives rise to the subneural gland. Later the cells of the dorsal wall of the posterior part of the neural canal begin to multiply rapidly; some of them become

their original arrangement as an epithelium bounding the canal; others, much more numerous, break up toward the ectoderm to form the dorsal portion of the [illegible] ganglion. This proliferation of cells is limited, at this time, to the [illegible]-posterior portion of the dorsal wall of the [illegible] canal. The brain cavity has now a thick ventral wall and a dorsal wall about twice as thick as the ventral.

At the time of the first appearance of the rudiment of the dorsal eye, the three regions, funnel, duct and brain, are clearly distinguished, the duct being a small round tube connecting the lumen of the funnel with the cavity of the brain. A description so far would answer almost equally well for either Salpa, Doliolum, or Pyrosoma, except that

the bottom, they do not leave the ventral wall of the neural canal. The dorsal, the brain cavity at this time is almost [illegible] dorso-ventrally, forming a narrow split separating the ventral third of the brain from the dorsal two-thirds. As the cells of the dorsal wall of the neural canal push up to form the dorsal part of the ganglion they do not at once make a solid mass, but they leave between themselves fine anastomosing lacunae canals, some of which open outward to the neural canal, while others are outward to the cavity around the brain. These lacunae are not mere chance spaces but have a quite definite appearance and persist for some time. In cross section the lacunae are seen to be separated for the most part by single rows of cells, resembling the [illegible] cells

between the lid lines of the higher Vertebrates. Soon the brain becomes solid, the lumina and also the central canal disappearing. When this change is nearly completed we have a condition almost exactly resembling that found in a nearly mature Ophidian. There is a slight antero-ventral process retaining a remnant of the disappearing brain cavity. This is still connected by a very fine canal with the wide lumen of the funnel. In the latter development the brain cavity and the duct wholly disappear and the lumen of the funnel is the only remnant of the neural canal. The duct disintegrates, as if pulled apart by the elongation of that region of the head, reminding one of the elongation of the [illegible] in Dolichos [illegible] which the cells are pulled [illegible]

intermediate [illegible] [illegible]. Neither in the half developed chain individual, nor in the adult can any trace of a duct opening into the funnel be found.

Certain other structures develop later that seem to bear the closest relation to the lateral communications between the sub-neural gland and the peribranchial chamber, described for Phallusia mammillata. At a time when the embryonic eye-disc has taken its perpendicular position, the roof of the [illegible] chamber, which up to this time has lain close to the ventral surface of the brain, begins to separate from the brain. Two small areas, however, remain contiguous with the brain, one situated at the right, the other at the left of the mid ventral point of the ganglion. As the wall of the [illegible]

chamber separates more and more from the surface of the ganglion. those portions of its wall which are adjacent to the two areas of adhesion are drawn out into two tubes leading from the ventral surface of the ganglion to the peribranchial chamber. The adult condition is reached by the considerable growth of these tubes which become greatly coiled, and by the flattening out into a hollow disc of the portion of each tube contiguous with the brain. The structure of the cells lining the tubes and hollow discs does not seem to indicate their function. They are smaller than the cells of the brain [illegible] oval in form have well defined nuclei surrounded by finely granular cytoplasm which under very high magnification show minute vacuoles. These may, or may not indicate secretory activity. The homologous

cells in Salpa Africana-maxima are almost surely glandular, so it is probable these cells in Cyclosalpa pinnata are more or less functional in secretion.

In close connection with the [illegible] ends of the tubes just described there are some masses of cells on each side. Of these two masses, the inner or anterior is composed of large cells with large nuclei, resembling closely the large ganglion cells that lie in the brain in the [illegible] region of the brain. The other posterior mass is composed of small cells with small nuclei, having the appearance of the smaller cells of the [illegible] part of the brain. These masses possibly develop simultaneously with the lateral tubes as outgrowths of the [illegible] areas of the brain. What present function, if any, they may have, or with what organs in other Tunicates they can be homologized, I have

unable to say. They may have no connection with the sub neural gland, but for convenience sake I describe them together.

In the *solitary form* of *Cyclosalpa, pinnata* the adult structures resemble minutely those described in the preceding pages. The early stages of development, too, are the same. I have not traced the development for other species.

The structure of the sub-neural gland and the organs connected with it in *both chain* and *solitary forms* of *Cyclosalpa Chamissonis* is the same as in Cyclosalpa pinnata. In other species there is a certain amount of variation. This is greater in the chain forms than in the solitary forms. *Salpa cylindrica*, solitary form, shows the same structure of the lateral tubes as Cyclosalpa pinnata,

but there are no ventro-lateral out-growths from the brain. In the chain form the right tube is reduced to a mere funnel-shaped pit in the pharynx wall. The left is more developed, but does not extend to the surface of the brain. It arises from the pharynx wall at the level of the posterior surface of the brain and runs forward and toward the middle line, ending blindly beneath the centre of the brain, without any enlargement comparable to the hollow discs found in Cyclosalpa pinnata. There are present in the chain form one pair of very slight ventro-lateral out-growths from the brain containing only the smaller kind of ganglion cells. Salpa scutigera. confoederata.

chain form, shows the lateral tubes and discs typically developed and a single pair of large-celled ventro-lateral outgrowths from the brain. I have not sectioned the solitary form. The chain form of Salpa bicaudata closely resembles that of Salpa scutigera-confoederata in the structure of the sub-neural gland and adjacent organs. In the chain form of Salpa democratica-mucronata there is no trace of lateral ducts or out growths from the brain. In the solitary form on the other hand the ducts are present in much the same condition found in Cyclosalpa pinnata. There are no out growths from the brain. In the solitary form of Salpa runcinata-fusiformis the tubes and hollow discs

are present and unusually large. Their epithelial lining is for the most part, lost, the walls of the tubes and of the greater part of the discs being formed only by the membrane continuous with the basal membrane of the wall of the pharynx chamber. There is in the chain form of this species an antero-ventral outgrowth from the ganglion. We shall see later that this is important. The chain form of Salpa costata-Tilesii shows a different condition of these organs. The wall of the peribranchial chamber remains attached to the whole ventral surface of the brain, forming a single large pit opening by a wide mouth to the peribranchial chamber. The cells of that portion of this pit,

which is attached to the ganglion, show the structure typical for the cells of the hollow discs. In this species also is the sub-neural gland an unpaired structure. The chain form of Salpa Africana-maxima shows the greatest development of the tubes and hollow discs. The latter are very large and are lined by an epithelium composed of a single layer of cubical cells whose outer ends are uneven whose protoplasm is granular and does not take up haematoxylin stain, and which have an appearance as if granular in function. On the dorsal side of the discs the epithelial cells are greatly increased in number, forming an irregular mass that [illegible] [illegible] the

lumen of the disc. In all species
the epithelium of the dorsal wall of
the disc is more developed and in
some species, (Salpa mucronata-
mucronata Salpa costata-Tilesii)
only this portion has an epithelial
lining that can be distinguished
in section. Probably there is a thin
pavement epithelium over the other
portions. The ducts, one on each side
as in other species, are unusually
large. They are lined by an epithel-
ium of columnar cells whose outer
ends are very irregular. I believe we
have in this species a gland which
is functional. The epithelium of
both discs and ducts has the charact-
eristic granular vacuolated protoplasm
and seems to be degenerating to

form the secretion. The fact that the hollow discs form the dorsal external walls of the great dorsal blood sinus which gives many branches to the dorsal lamina of gill renders it easily credible that these structures should function as a gland. If this gland be functional in this species it is the only case I have observed where the secretion could be considerable.

The nervous system of Salpa africana-maxima shows another feature which is of the keenest interest. We have seen that in the chain form of Salpa runcinata-fusiformis there is an antero-ventral outgrowth from the ganglion. This resembles the "wart-like", antero-ventral process from

the ganglion of Dolichum. In Sagitta Africana maxima there is a similar antero-ventral outgrowth from the ganglion and this is produced anteriorly as a rod of cells which runs forward beneath the eye, connecting the pharynx wall. It grows smaller, but still can be traced close pressed to the basement membrane of the pharynx wall, running on toward the ciliated funnel. It finally fuses with the pharynx wall, but can be traced for a comparatively long distance further as a very fine canal within the basement membrane.
Unfortunately the only two specimens of the Sagitta Africana-maxima I had to study were injured having been brought up from some depth

in the monster lines and having been in this way better drawn in one of these the ganglion was missing; in the other the ciliated funnel; so I have been unable to certainly establish the relation of this rod of cells to the ciliated funnel. I am convinced, however, that in this rod of cells we have the homologue of the tube which in Doliolum connects the ciliated funnel with the wart-like antero-ventral process from the ganglion. If this be so, we have, then, in Salpa Africana-maxima a condition that is found in Doliolum and in the young chain in Cyclosalpa pinnata. The nervous system of Salpa Africana-maxima is, then, in this respect, more primitive

than that of any other adult Salpa I have studied.

What is the relation between the ganglion, the sub-neural gland and its accessory structures in Salpa and the organs described in the first part of this section for Doliolum, Pyrosoma and Ascidians, and in favor of what relationships does the evidence derived from this source stand? The ganglion of Salpa has been regarded by Salensky and others as homologous with the whole central nervous system of the larval Ascidian. He has described three slight enlargements of the neural canal of the embryonic solitary Salpa, which he says correspond to the three primary vesicles of the Vertebrate

brain and to the three regions of the larval Ascidian neural canal — the sense vesicle, the visceral portion, and the caudal portion respectively. A careful comparison of the conditions in the different Ascidians and in Pyrosoma, Doliolum and Salpa seems to me, on the contrary, to indicate that the ganglion of Salpa is homologous with only the visceral portion of the Ascidian nervous system. In favor of this homology there are the following points:—

1. It is only in the visceral portion of the larval Ascidian nervous system that the ventral wall of the neural canal is thickened. Only that portion of the embryonic Salpa's neural canal, which has a thickened ventral wall persists as part of the adult ganglion.

2. The adult Ascidian ganglion is formed from the dorsal cells of the visceral

portion of the larval nervous system. The main portion (dorsal two-thirds or three-fourths) of the adult Salpa ganglion is derived from the dorsal cells of that portion of the embryonic nervous system which has a thickened ventral wall. The remainder is formed from the thickened portion of the ventral wall of the neural canal which persists. The ganglion would seem, then, to be certainly homologous with the ganglion of Ascidians and Pyrosoma; it being a structure of secondary formation in each, and having similar origin. In Doliolum, if we had full data for judging, it is probable a similar origin would be found for the dorsal part of the adult ganglion. The almost complete resemblance between the immature Salpa nervous system and that of the nearly mature Doliolum argues strongly in favor of the

3. The relation of the dorsal and ventral portions of the immature Salpa nervous system to the duct that turns into the funnel is much the same as the relation of the ganglion and sub-neural gland to the duct of that gland in the tailed larvae of many Ascidians, e.g. Amaroecium. In this connection the lacunae in the Salpa ganglion opening into the central canal of the nervous system and on the other hand, the connection between the larval Ascidian ganglion and the duct is suggestive.

4. The caudal portion of the larval Ascidian nervous system degenerates. In Salpa there is an absence of any caudal portion of the nervous system correlated with the absence of any normally developed tail.

5. The sense vesicle of the larval Ascidian is not found in any recognisable form in

either Salpa, Doliolum or Pyrosoma at any known stage of their development. It seems to be a special larval character secondarily acquired by the Ascidians. Whether it be secondary or ancestral for the whole group Tunicata it is unrepresented in Salpa, Doliolum and Pyrosoma, if it is represented at all, only by a few cells in the region of the junction of the brain with the duct that leads to the funnel. The three vesicles described by Salensky in the immature ganglion of Salpa scutigera-confoederata are probably to be regarded as secondary and having no morphological connection with the three primary vesicles of the vertebrate brain or with the three regions of the neural canal of the Ascidian tadpole. If the ganglia of Salpa and the Ascidians be homologous, as seems so evident, these so called vesicles in the ganglion of Salpa scutigera-confoederata

loose the morphological importance assigned
to them by Salensky.

If, then, we homologize the dorsal part of the ganglion in Salpa with the adult Ascidian ganglion, and the ventral third or quarter of the Salpa ganglion (the original thickened portion of the ventral wall of the neural canal) with the thick ventral wall of the visceral portion of the larval Ascidian nervous system, we are justified in saying that the Ascidian gland, which is formed from the thick ventral wall of the visceral portion of the larval nervous system, is represented in Salpa by the ventral portion of the ganglion. Of course this never functions in Salpa as a gland. The homology is strengthened by the presence of the lateral nerves in Salpa, which connect with the two hollow discs upon the ventral surface of the ganglion

with the branchial chamber. These seem to be very closely related to the communications between the sub-neural gland, and the peribranchial chamber found in Phallusia mammillata. The comparison is much more perfect by Herdman's description of two individuals of Phallusia mammillata in which the duct of the sub-neural gland leading to the ciliated funnel had atrophied.

The bearing of this homology upon the relation of the eye of Salpa to the larval Ascidian eye and the pineal eye of Vertebrates etc. is evident at a glance. Salpa's eye is a new structure wholly unrelated to the Ascidian eye. It develops from cells which have their origin in an entirely different region of the nervous system. It can not be homologized with either of the two Epiphyses of the Vertebrate brain, for it does not arise

directly from the central nervous system as do the latter, but arises from a secondarily acquired modified portion of the nervous system not represented in the vertebrate brain. For the same reason the accessory parts in the vicinity of the ganglion of Amaroucium cannot be homologized with the [illegible] sense organ, or the pineal eye of vertebrates as Julin claims, but if they be organs at all, they are probably homologous with the auditory or gastro-ventral sense organs of such genera as Cyclosalpa pinnata or Salpa costata-tilesii.

Does the condition of the nervous system and subneural gland of Salpa furnish any evidence as to the relationships of Salpa ~~to the other Tunicates~~? I have shown the almost constant resemblance between the nervous systems of Salpa and Doliolum, at a

certain stage of their development the nervous system of which passes through a Doliolum stage. This would be evidence then, as far as it goes, that Doliolum and Salpa had a common ancestor and that Doliolum stands the nearer to that ancestor. The nervous system of Pyrosoma, though a little more removed from that of Salpa still very closely resembles it. The two most important differences are the persistence of the neural canal in the adult Pyrosoma and the very slight degree of thickening of its ventral wall. The latter of these is a point of unlikeness from all other Tunicates and is probably to be regarded as secondary. In comparing the nervous systems of Ascidians Pyrosoma Doliolum and Salpa we find the latter then much more unlike than either of them is to the Ascidians. Of the latter there

Salpa appears to show the most resemblance with Ascidians because of the presence in these two alone of the lateral ducts to the peri-branchial chamber, but this point is not one from which alone certain degrees of relationship can safely be deduced, for the same structures may once have been present in Pyrosoma and Doliolum, though now they are lost in these genera. The presence of these structures in Ascidians and Salpa does strongly indicate that the common ancestor of the Tunicata had a neural gland with one or more pairs of communications with the peri-branchial chamber. Emphasis is given to this view by the fact that in Salpa africana-maxima, the chain form, whose nervous system shows the most primitive character, we have the greatest development of the gland.

The lateral ducts of the subneural gland in Phallusia mammillata connect with the peribranchial chamber, according to van Beneden and Julin, while in Salpa the lateral ducts connect with the pharyngeal or branchial chamber. This difference at first sight seems to preclude the homology of these organs in the two cases. But, still, after careful study, the structure seems to me that they may be homologous for several reasons. They have a decided superficial resemblance. They are located in the same region with reference to the ganglion. They have the same function; at least both are gland ducts. It is furthermore easy to conceive a shifting of position by which the lateral ducts originally opening to the peribranchial chamber came to open to the branchial chamber. The peribranchial and branchial

chambers in Salpa are laterally separated by no distinguishable boundary. I could not, from my own study of the adult salpa and the later stages of budding, ascertain whether the lateral ducts opened to the pharynx or to the lateral anterior prolongations of the peribranchial chamber. Professor Brooks, however, tells me that at this time (the time when the lateral ducts appear) the anterior portion of the peribranchial chamber is reduced to two very narrow lateral areas. The ducts, however, are not far from the median line. The whole formation of the peribranchial chamber in Salpa is so much modified that it is but a slight additional change to suppose that the openings of the lateral ducts of the subneural gland shifted their position a little more toward the median line, and into the region of the pharynx and that

later, this development being somewhat accelerated, the same to be formed before the anterior horns of the peribranchial chamber develop. The greater or less degree of concentration of the lateral ducts toward the mid dorsal line is seen in Salpa costata-Tilesii where the whole gland is but a median organ [illegible] on the mid line. The connection of the gland in Salpa with the branchial chamber instead of the peribranchial chamber seems then to be a comparatively slight secondary modification consequent upon the obliteration of the lateral walls separating the two regions.

The fact that in all but one of the eleven species studied this gland is paired is suggestive, but, in view of the fact that in Phallusia mammillata and in one species of Salpa (Salpa costata-Tilesii) it is unpaired, it is doubtful

whether in the common ancestor of the two the gland was a paired structure. The transition from a paired to an unpaired condition, or vice versa would be very easy. This is evident when we consider the mode of its development in Salpa. It is not probable that the earliest Ascidians had a gland of two-fold origin. The question then confronts us, which sort of subneural gland is the more primitive. Professor Herdman in his paper already referred to and in other more recent papers makes an interesting suggestion that "If the hypophysis cerebri was, as E. van Beneden and Julin think, a renal organ in the anterior part of the body of the primitive Chordata, its ducts – supposing it to be formed of several pairs of nephridia – would originally open on the sides of the body, and might have then

become implicated in the sinking in of the epiblast to form the atrial involutions, and so would come to open into the peribranchial cavity (a condition found in some Ascidians)". He says — "I would regard the connection between the duct, or one of the ducts, of the subneural gland and the dorsal tubercle as being secondary". According to this hypothesis Phallusia mammillata shows a transitional phase, most Ascidians have passed beyond and have lost the peri-branchial portion of the gland. Salpa then would retain or have reverted to the condition found in the more primitive Ascidians having a well developed peribranchial gland. It is possible that the presence in Salpa of the ventro-lateral outgrowths from the brain toward the lobular disc (of the peribranchial gland) indicate the partial retention of a process similar to that by which the subneural gland of [illegible]

is formed at the expense of the thick
ventral wall of the visceral portion of the larval
neural canal. The innervation of the larger-
celled pair of these outgrowths may indicate
that they were formerly, if not at present,
functional as ganglia in connection with a
well developed gland which arose from the
wall of the peri-branchial chamber.

On the other hand if a gland of neural
origin be the more primitive Phallusia mammil-
lata would still represent the transition from
this condition to the gland derived from the
wall of the peri-branchial chamber. I incline
to the former hypothesis, but, be this as it may,
Salpa has apparently retained or reverted to a
condition found in Phallusia mammillata,
since it shows traces of a gland of double
origin.

Molgula ampulloides has the well developed

lateral chambers, one on each side of the gland, which open through the duct of the gland into the pharynx by way of the ciliated funnel. These are of interest in this connection for they may correspond to the hollow disc of Salpa's gland. Molgula ampulloides would then represent a second transition between the condition in Phallusia mammillata and that of other Ascidians, since it has no lateral ducts. These comparisons are all hypothetical, with little direct evidence in their favor, yet they are well worth consideration.

The fact that in the Salpas we have present well developed eyes which yet can not be homologized with the larval Ascidian eye is suggestive in regard to a question which Professor Brooks discusses in the main portion of this monograph, namely, the question of Salpa's descent from

an attached Ascidian-like ancestor or from
a free swimming form like the Ascidian
larva. If, according to the latter hypothesis,
there had been no break in the free swimming
manner of life from the Ascidian tadpole to
its descendant Salpa, there would never
have been a time in its phylogenetic
development when an eye would not have
been needed, and so we would naturally
expect to find Salpa in possession of an eye
directly traceable to the Ascidian larval eye.
This, however, is not the fact. The eye of Salpa
is situated in a wholly different region of the
brain from that in which the larval Ascidian
eye is found. It would seem, then, more natural
to suppose that Salpa is descended from some
attached form, which having given up its
free swimming life, would have little use for
an optic organ and would therefore have lost

the eye which it is usually possessed. Salpa, on assuming a free-swimming habit, would need a visual organ: which, in fact, we find. The attached form, which the second hypothesis regards as Salpa's progenitor, would probably have lost the mostly developed sense vesicle which we see in the Ascidian larva, so that the free swimming ancestor which would have to develop an eye from another part of the brain. At the same time it would be the most natural that the new eye should develop about the same structure found in the eye possessed by its remote free-swimming ancestor, the Ascidian tadpole). This hypothesis explains then perfectly the fact that the eye of Salpa while having invariably the same structure as the larval Ascidian eye is found in a different part of the brain, [illegible] that the two are in no way homologous

The secondary manner of formation of the ganglion itself in Pyrosoma, Doliolum and Salpa would argue that they are descended from some common form which derived its ganglion from a secondary modification of the central nervous system [illegible] Ascidian-like rather than a tadpole-like form.

Appendix I

On page 117 I mentioned the conflict between Kowalevsky and Van Beneden and Julin in regard to the anterior opening of the neural canal into the peribranchial chamber in the Ascidians. Kowalevsky's statement that such a communication is present has lately been confirmed by Willey and Hjort, the two investigators working independently upon different species of Ascidians. There is, then, close agreement in this respect in all the four groups of Tunicates. Willey says – "As stated by Kowalevsky, the neuropore of the Ascidian embryo closes up at an early stage of development and the nervous system then consists of a completely closed tube with a dilated anterior extremity lying below the epidermis. Soon after the invagination of the stomodaeum and the subsequent perforation of the mouth the neural tube acquires secondarily

an opening into the stomodaeum." This statement is of interest in connection with Salensky's description of a similar closing of the neuropore in Pyrosoma, and the subsequent formation of a new connection between the gut and the lumen of the neural tube. It may still be true that in both Ascidians and Pyrosoma this secondarily established communication is but the reopening of the original neuropore. If the secondarily established neurenteric connection in Pyrosoma and Ascidians be not the primitive neuropore [illegible] then I was clearly mistaken in homologizing the ciliated funnel in Salpa with the neuropore in Pyrosoma, for then the definitive funnel in Salpa and Doliolum must be a structure different from the definitive funnel in Ascidians and Pyrosoma. The same reasoning however which I have [illegible]

first to regard the definitive [illegible]
[illegible] the definitive ganglion [illegible]
would now lead me to regard the definitive
funnel in both Ascidians and Pyrosoma
as the nervous centres.

Willey has shown also that the first
rudiment of the ganglion in Ciona intestin-
alis appears as a slight thickening of the
dorsal wall of the neural tube. This corresponds
exactly to what I have described for Salpa,
making still more indisputable the already
accepted homology between the [illegible]
[illegible] Ascidians, and
establishing, to my mind, conclusively the
homology between the visceral portion of the
neural tube of the Ascidian tadpole and
that portion of Salpa's neural tube from which
the ganglion is formed.

Appendix

While my paper was in press Professor Bütschli published a short note upon the eye of Salpa. I discussed briefly in the postscript the theoretical conclusions of his paper. I wish here to more carefully review it. Lest my criticisms should seem severe let it be borne in mind that Professor Bütschli expressly says that when he wrote his note he did not have access to the material upon which he had worked or to his preparations, notes, or figures, but that he wrote entirely from memory. Moreover his work upon this subject was confessedly incomplete, so that his suggestions were not the expression of his judgment carefully matured after thorough investigation, but were rather the conclusions toward which the work seemed to be leading him. The paper is

written in harmony with Professor Bütschli's characteristic clearness and suggestiveness, and his conclusions are so plausible that they deserve careful examination.

First, let me call attention to one or two anatomical points. Professor Bütschli shows that the retina is composed of two sorts of cells, the visual cells and the supporting cells (Stützzellen), and that the latter by their anastomosing processes form a network in whose interspaces the visual cells are held. As I have shown, this "network" is not a network of cell processes, but is really the deeply staining cell walls of the the inner-lying portion of the visual cells. In some cases the visual cells wholly or in part lose their columnar form and regular arrangement in a single layer. This arrangement may even become wholly

irregular that at the same time they assume an irregular shape. They still retain, however, the tendency to thicken their cell walls. The appearance seen in stained sections, which resembles an irregular network of cells is not a network of branching cells, but is formed by the thickened walls of the irregularly shaped (probably degenerate) cells which once functioned and perhaps still function as visual cells. Because of this tendency to thicken their cell walls I have throughout this paper called them rod cells. They are undoubtedly closely related structurally and physiologically to the rod cells in vertebrate eyes, which always show a similar thickening of their cell walls.

Professor Bütschli says the horse-shoe-shaped eye is secondary, having been

from a tricuspidate eye, of which it gives a schematic figure, as in illustration of how the horseshoe-shaped eye is derived from the tricuspidate form it is very evident that our drawings agree in its form. There is no
Eye
among the [illegible] Salpa [illegible] which his description (tricuspidate [illegible]) could accurately apply [illegible] be studied from an aberrant species which I have not seen. We must [illegible] to such an eye as is found in the chain form of Salpa runcinata-fusiformis or some of its nearest allies. In this form the large dorsal eye is either horseshoe-shaped or globular, and answers roughly to his description. Professor Bütschli regards this as the primitive form of Salpa eye, basing this conclusion on certain anatomical features which are seen in his erroneously described. He says — "Die Hauptmasse des [illegible] [illegible]

Eye)" wird von einer lichtempfindlichen Retina gebildet, deren Zellen der freien Wölbung des Flügels entsprechend etwas radiär zu der Oberfläche gestellt sind. An seiner basalen Peripherie wird dieses kuppe=artige Organ von einem ringförmigen Gürtel von Pigmentzellen umzogen, x x x x. Das erwähnte einfache Auge empfängt seinen ~~Augen~~ Nerven fasern direct von unten an dem Gehirn". The structure of this eye is not so simple as the description says. In many of the three species I have studied as the rod cells all have the same arrangement. In every case, as I have shown, where the eye is globular or spindle-shaped, the rod cells of the posterior portion of the eye have their innervated ends distal from the ganglion, while in the anterior portion of the eye this arrangement is reversed. The pigment cells

also show a different arrangement in their two portions and do not form what can be called a simple ganglion at the base of the eye, but the cells instead of becoming the commissural fibres direct from the ganglion region then form a large optic nerve which passes up on the dorsal surface of the posterior part of the eye and then around to the ventral side of the anterior portion. Thus three mistaken characters of its description are them of the four points he emphasises to show the primitive character of this form of eye. The fourth point is its simple shape.

Again we would not naturally expect to find the primitive type of simple eye in the chain form of [illegible] since the chain individuals are aberrant and are derived from the solitary [illegible] forms.

a peculiar kind of budding. The chain individuals then being secondary, the presumption is strong that their type of eye would be secondary.

Emphasis is given to this view by the fact that the same type of eye, (horse-shoe-shaped) is found in the solitary form of each species, while the chain form of each species has a type of eye peculiar to itself.

The secondary nature of the "chain" type and of all other sorts found in the chain salpas and the primitive character of the horse-shoe-shaped eye is conclusively shown by the fact that the eye of the chain individual passes through an ontogenetic stage when in form, though of course not in histological character, it closely resembles the horse-shoe-shaped

Eye of the solitary Salpa.

Professor Bütschli's suggestions as to the probable primitive mode of origin of the vertebrate lateral eyes are based upon the secondary nature of the horseshoe-shaped eye and its manner of development from the "Hügelartig" eye. If the latter be overthrown the former are without foundation.

The most important point, however, is not that for certain special reasons founded upon the comparative anatomy and development of the Salpa eye the relation suggested between this organ and the vertebrate lateral eyes is mistaken. It is fundamentally erroneous to homologize the eye of Salpa with the eye of any other Chordata. The Salpa eye is developed from a portion of the nervous system, which is

derived in a very secondary manner
from ~~the hind brain of the third primary vesicle of the anterior~~ a portion of the
brain not represented in the Vertebrate.
The eyes of all other chordates are developed
from the walls of the first primary vesicle.
Professor Bütschli's hypothesis is supported
then by the character of the eye in the
chain and solitary forms, its manner of
development and by the fact that it is
developed from a portion of the nervous
system not represented in any Vertebrate.

Appendix III

Since my paper was — since Dr. E. Göppert has published an excellent paper upon the eye of Salpa. The author had evidently not seen my preliminary abstract, so it is the more gratifying to see how completely, so far as he has gone, he confirms my results.

He gives a good account of the anatomy of the eye of both the chain and the solitary forms of Salpa africana-maxima, Salpa runcinata-fusiformis, Salpa pinnata, and Salpa democratica-mucronata and Salpa scutigera confoederata. His description of the minute internal anatomy of the rod cells, especially as regards the so-called phaeospheres, is more elaborate and thorough than my own.

There are two or three points in which I must take exception to his statements, and few others

upon which I need comment. There is however one fundamental disagreement between our observations, namely in regard to the innervation of the rod cells. I may state at once that if I had not had opportunity to study the development of the eye I would have been unable to speak with any certainty of the innervation of one portion of it — that portion upon which our observations disagree. In his

In his description of the large dorsal eye of mature individuals of Salpa africana-maxima, Salpa pinnata and Salpa runcinata-fusiformis Göppert says that in the posterior portion of the eye the rod cells receive the innervating fibres into their thin walled ends, while in the anterior ~~end~~ portion they receive the innervating fibres into their thick walled ends. Reference to my figures 7, 8 and 9, Plate I will show that this is a mistaken state-

ment. Figure 7, on' shows the large [illegible] the nerve above one of the posterior limbs of the eye (E'), in which region it innervates the thin walled ends of the rod cells directly beneath it. Figure 8 shows the innervation of the third region of the Eye (E'''). That the rod cells of this region receive the innervating fibres into their thin-walled ends is more clearly shown in figure 7, Plate II. Figure 9, Plate II shows another bundle of fibres from the optic nerve, on''', passing down between the two posterior limbs of the eye (E) to innervate the ventrally placed thin-walled ends of the rod cells of the second, the anterior, portion of the eye (E''). The rod cells then in all regions of the eye of the chain Cyclosalpa pinnata are innervated at their thin-walled ends, the ends distal from the pigment layer, [illegible] fundamental difference in the innervation of the different

regions of the eye as Hesse describes would be utterly inexplicable. It is but fair to say that in the adult eye the fibres of the optic nerve are much more closely fused to the rod cells than in the immature individuals. It is therefore a matter of great difficulty to determine the innervation from study of serial sections of the adult. The minute fibres innervating the rod cells of the anterior portion of the eye can not be traced in sections. The fibres of the nerve seem to stop at the junction of the posterior limb of the eye with the anterior curved portion. That this appearance is deceptive is shown by my sections of the immature individuals. But even in the absence of the actual proof I have brought forward we would be justified in believing that the innervation in all regions is uniform unless there were

much more definite observations to the contrary than any Dr Jöppner has made.

In the immature chain Cyclosalpa pinnata it is plainly seen that the rodcells in all regions are innervated on their thin walled ends. In the adult chain Cyclosalpa pinnata the innervation of the anterior region of the eye can not be made out. In other chain Salpas of this pinnata group the innervation of the anterior region of the dorsal eye can no more be made out in the adult than in the adult Cyclosalpa pinnata. The innervation of the posterior region is plainly seen to be the same as in the latter species. The anterior portion of the dorsal eye is clearly homologous in all these species. In consideration of these facts we must believe that the innervation

in all the species is as in Cyclosalpa pinnata. In the chain salpa tuberculata-mucronata, which I have shown belongs to the pinnata group, since the dorsal eye is here unused, Göppert himself says the rod cells of all regions are innervated from their thin-walled ends. In the more primitive group including Salpa scutigera-confoederata and Salpa bicaudata, my figures show as clearly as can be shown from sections of the adult eye that the manner of innervation is the same. The innervation of the anterior rows of the eye of the solitary form is also difficult to make out, but since the rod cells of the posterior curved portion are clearly seen to receive the fibres in to their thin-walled ends there is no room for doubt that the rod cells of the anterior portion also are inner-

vated at the thin walled ends.

Göppert describes in cyclosalpa pinnata, solitary form a connection of the nerve fibres with the ends of the rod cells near the pigment layer, while in the anterior part of the retina of the chain Salpa africana-maxima he says the nerve fibres connect with the cells of the intermediate layer. His whole account of the innervation is anomalous.

Göppert's description of the histology of the eye of the solitary Salpa africana-maxima (which I was unable to study in section) agrees very closely with my description of the histological condition of the eye of the solitary Salpa runcinata-fusiformis, thus confirming the view that these two species are very closely related.

Of the connection between the rod cells and intermediate cells in the larger eye of the

chain Salpa Africana-maxima Göbel(?) says "Ich glaube mit aller Sicherheit behaupten zu können dass jede der grossen Zellen (red cells) durch ihren die mittlere Ektodermschicht durchsetzenden Fortsatz mit einer dieser kleinen Zellen" intermediate cells" verbunden ist." This confirming the opinion I had stated. His figure illustrating the point is, however, more diagrammatic than any of my sections.

That Brooks fails to see the homology between the regions of the egg of the chain salpa scutigera-confoederata with those of the egg of any other species is only natural since he did not clearly grasp the idea of the removal of the egg in most species and the consequent change in the course of the [illegible] wire. It is interesting to note that he does suggest, though not

with much confidence that, there has perhaps been a forward binding of the eye in the chain individuals, a thing which I had already shown to be a fact.

Leuckart's statement, which Gippert quotes apparently with approval, that the pigment layer is always superficial immediately under the epidermis is clearly shown to be inaccurate by my figures 7 and 8, Plate I; 2, Plate VI; 10, p, Plate VIII.

By Gössner emphasises the statement that in the dorsal eyes, unlike the retina cells of the different regions receive light from but one direction, thus weakening the evidence of accurate vision. Whether the facts of the anatomy lend support to this view I am unable to decide. I am much less able to accept as true the author's assumption that the masses of rod-like cells which

nerve ganglion and an eye associated with pigment are functional optic organs. The author's casually stated opinion that the lateral chambers of the subneural gland which he observed, are organs of hearing is but a sample of the far too many statements without study made by students of the Tunicates which have only added to the confusion.

I do not wish my criticism to imply any failure to appreciate the value of [illegible]'s anatomical observations which are in the main very accurate.

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Explanation of Plates
Omitted in this copy.

The author of this thesis was born
March 12th, [illegible] at [illegible], which has
since been his home. He studied at the
Central College near [illegible], Franklin Co., and
[illegible] for [illegible]
took his [illegible]
[illegible]
since that time he has been [illegible]